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# Ontogeny of the rest-activity rhythm in the Wild boar

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## Abstract

Continuous biotelemetry records of the wild boar (*Sus scrofa* L.) under natural conditions were used to study the ontogeny of its rest-activity rhythm. A nycthemeral component was found in the rhythms of all individuals investigated, both juveniles and adults at the various stages of the reproductive cycle. In contrast, ultradian rhythms were typical of immaturity; they were present in juveniles and in females accompanied by unweaned piglets and disappeared in adult females with weaned piglets or without piglets and in adult males. The detected ultradian rhythms had periods of approximately 3 hours or multiples of 3 hours according to age for juveniles and to the lapse of time since farrowing for females. Results are discussed with respect to uniform influences of internal processes and environmental factors on the individual behavior.

## Introduction

According to Aschoff (1957), animals possess an endogenous sleep-wake rhythm which is solely influenced by the fluctuations of the internal environment. Biological events, such as oestrous (Cushing 1985), rut (Hansen 1984), parturition (Mauget 1980), weaning (Astic et al. 1979) and aging (Büttner 1980) are the principal factors modifying this internal rhythm. But this primitive rhythm is not often detectable since, in wild animals and especially in ungulates, many activities are modified in frequency, amplitude and time of occurrence by the effect of ambient physical and biological factors. The main physical factors modifying endogenous rhythms are temperature (Bigler 1974) and photoperiod (Campbell and Tobler 1984); the biological factors include food availability (Arnold 1964), the influence of predators (Meddis 1975) and of congeners (Harcourt 1977).

The aim of the present study was to investigate variations of the rest-activity rhythm in free-ranging wild boars, dividing the studied animals into three groups: (i) adult females between farrowing and weaning (2–3 months, Newberry and Wodd-Gush 1985), (ii) juveniles (from weaning to 9 months, Spitz 1992) and (iii) adult females after weaning of their piglets, adult females without piglets and adult males. This classification allowed us to identify some rules about the influence of age and of farrowing on adult females.

## Material and methods

### Study areas

The data were collected from two study sites in southern France (i) in the Camargue from 1985 to 1987, where the technique was developed and checked (Janeau and Hachet 1991) then (ii) in the Caroux and Montagne Noire massifs from 1989 to 1991. The Camargue is a flat area (around sea level), with a Mediterranean type climate; the area consists of a similar proportion of crop lands and marshes, with very small scattered woods and shrublands (Dardaillon 1984). The Caroux Espinouse and Montagne Noire massifs belong to the same extended mountain area; elevation ranges from 200 to 1 200 m a. s. l. The climate is also Mediterranean, with montane influence, according to altitude and orientation. The vegetation is diverse (holm oak, chestnut, conifer or beech stands, various types of heathlands, chapparal and grasslands; Auvray 1983; Anonymous 1979).

### Data acquisition

The boars were captured and fitted with leather collars, using extendible type for young animals, onto which a radio emitter was fixed. The animals were classified according to their weight as juveniles or adults (Pepin et al. 1986; Spitz 1992). The exact dates of farrowing were deduced from the daily movements of the females (Janeau and Spitz 1984), since the emitter collar also provided radio locations.

To record activity, an inclination sensor, linked to the emitter, transmitted information to an automatic acquisition system working in real time (Janeau et al. 1987). The set-up was composed of omni-directional antennas, receivers and two interfaces; the first transformed the radio signal into a 5-volt signal and the second was for input management (up to 15 channels), dating the occurrence of the data and transmitting them to a microcomputer for storage. Each continuous record was analyzed with a time step of one minute and a predominant activity type attributed to each step. As recommended by Bubenik (1960), the only distinction made in the present report was between real rest and activity in a general sense (including locomotion, feeding and social activities).

Thirty-eight sessions of 24 hours, some consecutive, were recorded on 14 animals, 7 adult females at various stages of the reproductive cycle (in winter, spring and summer), 2 adult males (in winter), 3 juvenile males (between 6 and 8 months of age) and two slightly younger juvenile females (3 to 4 months) in spring and summer. Ten records of 48 hours were considered (Tab. 1). In the study of the 24-h sessions the individuals followed for 48 hours were only taken into account for one of the two consecutive 24-h periods. For a given individual, only records separated by at least 5 days were considered (Tab. 2).

### Data analysis

Classical methods (Broom 1979) of detecting rhythms could not be used with these data. The 48-h data samples were processed with a time step of 15 minutes and those of 24 hours with a time step of 5 minutes to give a sufficient number of events in each series. Each interval was attributed a number corresponding to the total number of minutes of activity it included. A 48-h record was then reduced to a chronological series of 192 values and a 24-h record to a chronological series of 288 values. The chronological series were analysed on the principle of the auto-correlation method. For each shift of the series with itself, we calculated the proportion of cases (pobs) for which the two corresponding values were below or greater than the median of the studied series (pobs + qobs = 1, qobs was the proportion of the complementary event). For each series of n events, n/3 shifts were made.

The observed proportions were compared to the limits of the confidence interval of a theoretical proportion. This theoretical proportion was determined assuming the null hypothesis of an equiprobable distribution of the values with respect to the median ($p = q = 0.5$). In this way, each shift for which the observed proportion was outside the limits of the interval of confidence enabled the identification of a significant period with an error risk fixed at 0.05. For each series, we obtained several groups of values outside of the confidence interval, and calculated a mean period for each group (values below the confidence interval gave 1/2 periods). All mean periods obtained for each group corresponded to a fundamental period and its harmonics. Only fundamental periods were taken into account.

Figure 1 shows a graphic representation of a chronological series recorded on a juvenile female (97-days old) and of the observed proportions according to the number of shifts.

The $\chi^2$, Mann-Whitney tests and Spearman's coefficient were used to compare the samples.

## Results

### Nycthemeral rhythms

From the 48-h records, rhythms were detected with a period of 24 h or less. Table 1 reports the mean periods obtained with respect to the biological characteristics of the animals. All the individuals studied showed a rhythm with a nycthemeral component. These

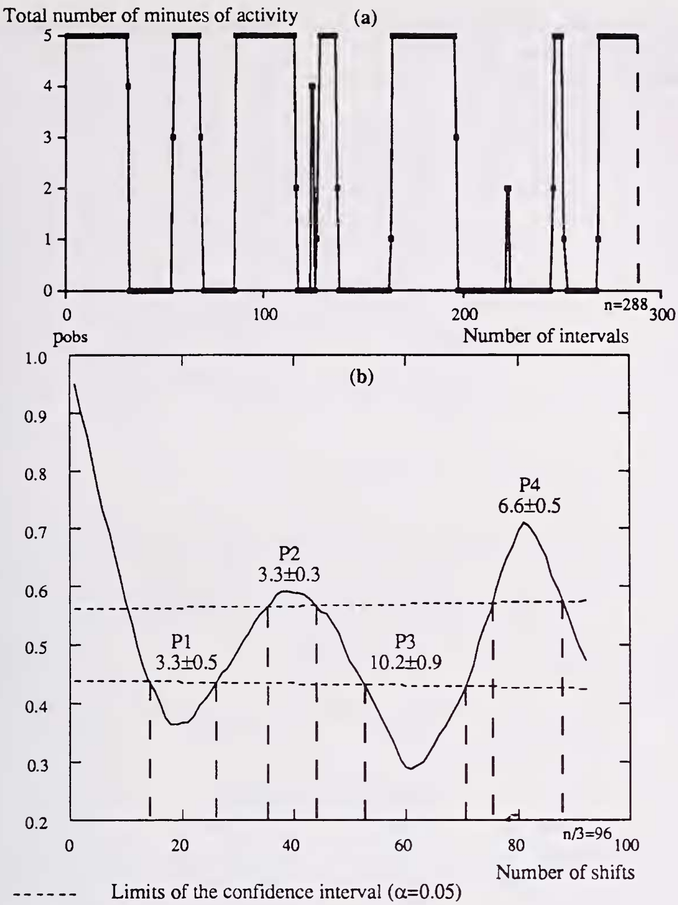


**Fig. 1.** Example of (a) the original chronological series (median = 5) and (b) the data analysis of the 24-h session on the 97-day-old juvenile. pobs = proportions of cases for which the values of the original and the shifted series were both below or greater than the median. All obtained ultradian periods P and standard deviations are in hours.

mean periods were between 21 and 24 hours (Tab. 1). The data obtained on a per class basis were insufficient (2 records on adult females with unweaned piglets, 6 on juveniles and 2 on adults outside the farrowing season) to test significant differences in the durations of the periods obtained.

### Ultradian rhythms

From 24-h samples, only rhythms with a period of less than 12 hours could be detected. We assumed that the weaning of piglets had an influence on the rhythm of the mother. Thus the classification of animals that was used in table 2 differenciated adult females according to whether they had weaned or unweaned piglets. Ultradian rhythms (Regal and Connelly 1979) were more often observed ($n = 10$, $\chi^2 = 3.6$, dl = 1, $a < 0.05$) in females with unweaned young and in juveniles than in other adults (including females with weaned piglets). According to our findings, the complete disappearance of the ultradian rhythm for the adult females seems to occur before the 4 h month after farrowing (Tab. 2), but an ultradian component still subsists in juveniles at the 7 h month of life.

**Table 1.** Mean circadian periods (in hour) and standard deviations using 48-h records.
Age or elapse of time since farrowing are noted in days (d) or in months (m).
AF: adult female; AM: adult male; J: juvenile.

| Animals | Mean period |
|---|---|
| AF 35 d | 21 ± 1 |
| AF 80 d | 24 ± 2.5 |
| J 80 d | 23.5 ± 4.5 |
| J 80 d | 23.2 ± 4.6 |
| J 6 m | 22 ± 2.5 |
| J 6 m | 21.1 ± 2.4 |
| J 7 m | 22.5 ± 1.5 |
| J 7 m | 22 ± 4.2 |
| AF 130 d | 22 ± 4.25 |
| AM | 24 ± 0.7 |

**Influence of age on ultradian rhythms**

Tests were made for the occurrence of significant differences in the mean ultradian periods obtained – at least when they did exist – in juveniles. The Mann-Whitney test showed that the mean periods of ultradian components of 6-month-old juveniles were significantly (n1 = 3, n2 = 7, U = 18, $a < 0.02$) longer than those of 3-month-old juveniles. Mean period durations tended to be around 3 hours for the youngest animals, and around 6 hours for 6-month and 7-month old juveniles.

**Table 2.** Mean ultradian periods (in hour) and standard deviations using 24-h records. Records showing no ultradian period are also reported (/).
Age or elapse of time since farrowing are noted in days (d) or in months (m).
AF: adult female; AM: adult male; J: juvenile.

| Adult females with unweaned | | Juveniles | | Others adults | |
|---|---|---|---|---|---|
| Animal | Mean period | Animal | Mean period | Animal | Mean period |
| AF 00 d | 6.7 ± 1.2 | J 81 d | 3 ± 0.3 | AF 100 d | 11.6 ± 1.2 |
| AF 00 d | 0.7 ± 0.1 | J 81 d | 5.6 ± 0.3 | AF 105 d | 10.1 ± 1.5 |
| AF 15 d | 2.9 ± 0.1 | J 97 d | 3.3 ± 0.6 | AF 120 d | – |
| AF 35 d | 2.6 ± 0.9 | J 6 d | 5.7 ± 1.3 | AF 130 d | – |
| AF 50 d | – | J 6 d | 6.5 ± 0.2 | AF 6 m | – |
| AF 51 d | 6.2 ± 0.7 | J 6 d | 5.8 ± 1.3 | AF | – |
| AF 65 d | 2.7 ± 0.7 | J 6 d | – | AM | – |
| AF 80 d | 4.7 ± 0.5 | J 7 d | 6.7 ± 1.4 | AM | – |
| AF 80 d | 3.8 ± 0.8 | J 7 d | 6.6 ± 0.4 | | |
| AF 86 d | – | J 7 d | – | | |

**Influence of distance from farrowing on ultradian rhythms**

For the adult females, we examined the relation between the duration of the mean ultradian periods and the lapse of time since farrowing by way of Spearman's correlation (Tab. 2). Mean period duration tended to increase with the elapse of time since farrowing (n = 10, Rho = 0.567, z = 1.709, $a < 0.05$); they were around 3 or 6 hours for females with unweaned piglets (one farrowing female excepted) and approximately 10–11 hours for females with weaned piglets.

## Discussion

A nycthemeral component is typical of all studied wild boars, juveniles and adults at various stages of the reproductive cycle. The presence of such a component, regardless of the study area or the season, prompts us to envisage it as a circadian (Halberg 1959) rhythm.

The latter is commonly brought about by periodic factors in the environment, commonly called Zeitgeber (Aschoff 1957). In adult wild boars, as in many other ungulate species, sunset appears to be the principal factor involved (Mauget 1980; Niethammer and Krapp 1986; Janeau et al.1994).

In contrast to this circadian rhythm, the presence of ultradian rhythms is characteristic of the juvenile phase. The most frequently quoted hypothesis is that these ultradian rhythms are imposed by the metabolic and physiological requirements of the newborn. In contrast, Dallaire et al. (1974) and Hoppenbrouwers and Sterman (1975) estimated that the ontogenesis of the sleep rhythm in young mammals appears to be linked to the maturation of the central nervous system. In the child, de Roquefeuil et al. (1993) hypothesize that the period of the ultradian rhythm would be unstable and would tend to lengthen during individual development, sometimes progressively and sometimes by "fits and starts". Schmid et al. (1988) also state that the stabilization of distinct circadian rhythmicity is an indication that the ultradian rhythmicity, until then predominant, was superseded by nycthemeral rhythmicity.

In the same way, the rest-activity rhythm in the young wild boar could initially be represented by a primitive ultradian rhythm of the order of 3 hours and by a circadian one (this latter rhythm could be induced by maternal transfer of photoperiodic information, Horton and Stetson 1992). Progressively, through the ontogenetic processes, such as maturation of the nervous system and the disappearance of the various constraints linked to suckling, the ultradian rhythm would tend to disappear; this dissapearance would be due to an increase in the fundamental period towards its harmonics until it was superceded by the nychtemeral rhythm. Adult females which had just farrowed would recover this primitive rhythm by induction from the newborn (induction of suckling phases, Gill and Thomson 1955), or modification of their hormonal state.

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## Zusammenfassung

***Ontogenese des Aktivitäts-Rhythmus beim Wildschwein***

Kontinuierliche biotelemetrische Aufzeichnungen am Wildschwein (*Sus scrofa* L.) unter natürlichen Bedingungen wurden zum Studium der Ontogenese des Aktivitätsrhythmus genutzt. Bei allen untersuchten Individuen, ob juvenil oder adult in verschiedenen Stadien des Reproduktionszyklus, wurde eine nychtemerale Komponente gefunden. Ultradiane Rhythmen traten bei Juvenilen sowie bei Weibchen mit Jungen auf. Sie fehlten bei adulten Bachen mit abgesetzten Jungen oder ohne Junge und bei adulten Keilern. Die gefundenen ultradianen Rhythmen hatten Perioden von circa 3 Stunden oder harmonische Schwingungen von 3 Stunden entsprechend der Distanz zum Wurftermin.

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